

DEVELOPMENTAL DIFFERENCES IN THE TEMPORAL SUMMATION
OF TRANSIENT AND SUSTAINED AUDITORY STIMULI

By

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Dedicated to my parents,

Ella Dora Blumenthal and Otto John Blumenthal,
for giving me the tools I need to get the job done.

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By

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The present study measured the startle eyeblink electromyographic (EMG) response to transient and sustained auditory stimuli in human adults and newborns, to assess immaturity of temporal summation in newborns. Stimuli were broadband noise bursts (20Hz-20KHz) with fast (<0.1 ms) rise times. In Experiments 1 and 2 adults received 95 dB(A) stimuli, in 13 stimulus conditions. One stimulus was 3 ms long, six varied in duration from 20 to 100 ms in Experiment 1 and from 30 to 55 ms in Experiment 2, and six consisted of pairs of 3 ms stimuli at onset-to-onset intervals analogous to the durations used. In Experiment 3, newborn infants (7-36 hours old) received 100 dB(A) stimuli analogous to those of Experiments 1 and 2. Startle amplitude increased for single and paired stimuli up to 40 ms in adults and 50 ms in infants, above which single stimuli maintained this response amplitude while the second pulse in a pair was not effective. Within these summation windows, single stimuli were not significantly more

effective than analogous paired stimuli. Startle probability increased for single stimuli up to 20 ms in adults and 35 ms in infants, above which no significant age difference was found. Single and paired stimuli were equally effective up to 45 ms for adults and 20 ms for infants. For paired stimuli, intervals of 20-45 ms were equally effective in adults, and intervals of 20-50 ms were equally effective in infants, with the second pulse at longer intervals having no effect, but probability for infants was lower than that for adults at all intervals tested. Response latency decreased as stimulus duration increased to 20 ms, for adults but not for infants, and no significant effect of interpulse interval on latency was found at either age. The window for transient summation is narrower in adults (40 ms) than in infants (50 ms), and brief stimuli are more effective in adults than in infants. These data suggest that the transient system is immature in infants and that these developmental differences are illustrated in different ways by startle amplitude, probability, and latency.

CHAPTER I INTRODUCTION

Transient and Sustained Systems

The processing of sensory input may occur in different ways for transient and sustained stimuli. Transient stimuli activate onset-sensitive response systems (detection), while sustained stimuli activate response systems which are sensitive to more prolonged stimulus attributes (identification). A stimulus with both transient and sustained properties may activate both types of response system. This transient-sustained dichotomy has been found for auditory (Graham, 1979), tactile (Verrillo, 1968), and visual (Schwartz & Loop, 1984) input, and underlying neurological mechanisms have been proposed in each modality (Gersuni, 1971; Gescheider, 1976; Hickey, 1977). Also, the mechanisms underlying this dichotomy are believed to develop at different rates, at least in the auditory (Graham, Anthony, & Zelgler, 1983) and visual systems (Hickey, 1977; Norman, Pettigrew, & Daniels, 1977).

One way in which transient and sustained systems differ is in their temporal summation abilities, with rapid summation occurring in transient systems, and longer-lasting summation occurring in sustained systems. In the auditory system, temporal summation has been investigated using behavioral scaling (Zwislocki, 1969), single unit responding (Gersuni, 1971), and brainstem reflex elicitation (Marsh, Hoffman, & Stitt, 1973). The present study used the acoustic startle

reflex to assess developmental differences in temporal summation in human transient and sustained systems.

Temporal summation involves the integration of sensory input over time. This is illustrated by the fact that the effectiveness of a stimulus can be increased by increasing its duration, to a point. The duration above which no further summation occurs is called the critical duration, and is the point at which the summation function (perception plotted as a function of stimulus duration) reaches asymptote. Also, a pair of stimuli can be more effective than a single stimulus, and this increases as interstimulus interval decreases. The interval below which further reductions of interstimulus interval have no greater effect can be considered a critical interval, analogous to the critical duration. Both the critical duration and the critical interval are the points at which their respective functions of sensation plotted as a function of time reach asymptote. Temporal summation has been found in several sensory modalities, using a variety of experimental techniques.

Psychophysical investigations of visual perception show that brightness increases as stimulus duration increases to 500 ms, but not beyond (Stevens, 1966). As stimulus intensity increases, this critical duration decreases, but the slopes of the summation functions are parallel across a range of intensities. This suggests that summation occurs until some specific amount of input has occurred, and this amount is reached more rapidly by stimuli of higher intensity. Temporal summation may asymptote due to sufficient "area under the curve", as determined by the stimulus envelope.

Schwartz and Loop (1984) have shown that visual perception may involve two partially independent systems, a chromatic and an

achromatic system. The chromatic system is sensitive to stimulus duration, showing summation functions with critical durations of 500 ms. The achromatic system is believed to be sensitive to transient stimulation only, showing no effect of duration in the range tested (43-1000 ms). These systems may be differentiated at the neuronal level, in that retinal ganglion cells with transient discharge patterns (Y-cells) are more common in the periphery, where achromatic stimulation is more pronounced (Hirsch & Levant, 1978). Ganglion cells with sustained discharge patterns (X-cells) are more common in and around the fovea, where chromatic activation is maximal. This indicates that the differential temporal summation of chromatic (sustained) and achromatic (transient) systems may be due to underlying neurological distinctions.

For intermittent visual stimuli, brightness decreases as interstimulus interval increases beyond the critical flicker fusion threshold (Bartley, 1969). Below this threshold, temporal summation occurs to prevent the brightness from decreasing when the stimulus is not on continuously. In the visual system, the critical interval is illustrated by the critical flicker fusion threshold.

Temporal summation has also been shown for both taste perception (Bujas & Ostojcic, 1939, as cited in Marks, 1974), and proprioception (Brown, 1966, 1968). Brown rotated subjects, varying the duration and acceleration of the rotation. The perceived magnitude of the rotation increased as the duration of the rotation increased, at a range of accelerations. As acceleration was increased, the effect of duration on perceived magnitude of rotation reached asymptote earlier, similar to

the finding on the visual system that critical duration decreases as stimulus intensity increases.

For tactile stimuli, two patterns of temporal summation exist. If Pacinian corpuscles are present, summation occurs with a critical duration of 500-1000 ms (Gescheider, 1976; Verrillo, 1968). This critical duration decreases as stimulus intensity increases, just as in the visual and proprioceptive systems. If Pacinian corpuscles are not present, summation still occurs, but with a critical duration of less than 1 ms (Higashiyama & Tashiro, 1983). This is analogous to the rapidly summing achromatic (transient) and slowly summing chromatic (sustained) systems found in vision. Both visual and tactile systems are distinguished by functional differences at the periphery which result in qualitatively different stimulus processing.

In the auditory system, psychophysical methods have been used extensively to illustrate temporal summation. Loudness matching has been used to show that increasing stimulus duration results in decreased threshold, up to a critical duration of 200 ms (Scharf, 1978). Critical duration decreases as stimulus intensity increases (Richards, 1976), but the slope of the summation function is the same across a wide range of intensities (Small, Brandt, & Cox, 1962; Stevens & Hall, 1966), as is the case for tactile, proprioceptive, and visual stimuli. For pairs of brief pulses, threshold increases as interpulse interval increases, up to 200 ms (Scharf, 1978; Zwislocki, 1960). Using psychophysical methods, the critical duration and critical interval for auditory temporal summation appear to be the same.

While the use of loudness matching in assessing temporal summation has provided much information, this technique is not without problems.

Differences in subject criteria used in the matching tasks can result in variable findings. For example, when subjects are told to match on the basis of the loudness at the onset of a stimulus as opposed to the total loudness of the stimulus, differences in stimulus duration effects are found (Zwislocki & Sokolich, 1974). These problems could be avoided by using techniques which are less susceptible to cognitive influences, such as psychophysiological or neurophysiological responses.

The investigation of auditory temporal summation at the neurophysiological level has led to the identification of two types of neurons in the auditory pathway which differ in their characteristic discharge patterns to stimuli (Gersuni, 1971; Radionova, 1971). Short time constant (STC) units illustrate a transient discharge at stimulus onset (and at offset, in some cases), while long time constant (LTC) units discharge in a sustained fashion, throughout the duration of the stimulus. These units are also sensitive to different stimulus parameters, with LTC units being sensitive to stimulus duration, but not to rise time, while the opposite is true of STC units. The two types of units show different patterns of temporal summation, with STC units having very brief critical durations (a few milliseconds), and LTC units having much longer critical durations. These units are found at all levels of the auditory pathway, and may be organized into functional systems resulting in differential processing of transient and sustained stimulus attributes. In this respect, the LTC and STC systems are analogous to Pacinian and non-Pacinian systems in tactile processing, and to chromatic (X-cell) and achromatic (Y-cell) systems in visual processing. All three modalities illustrate distinctive

transient and sustained systems which possess different temporal summation properties.

Evidence for auditory temporal summation has also been found at the level of the receptor (hair cell) in monkeys (Kletschy & Stengrevics, 1972). Period histograms of receptor activity, which are correlated with positive excursions of the stimulus waveform, decay more slowly than does the stimulus, with a lag of .1 to .2 ms. This implies that some integration may be taking place at the hair cell, resulting in a prolongation of the half-wave rectified receptor potential.

Temporal summation appears to be a fundamental property of several sensory systems. This summation may vary with the stimulus envelope, until some maximal amount of summation has occurred, since critical duration decreases as stimulus intensity increases, in several sensory modalities. Also, in the tactile, visual, and auditory systems, differential summation of transient and sustained stimuli can be found, suggesting the possibility of analogous underlying mechanisms in the three systems. Investigations of such mechanisms would be aided by a response which is sensitive to small stimulus changes, and which can be found across a range of ages and species. The startle reflex is such a response.

The Startle Response

The use of the startle response as a means to assess temporal summation can be recommended for several reasons. This response is very reliable, shows considerable plasticity and sensitivity to stimulus conditions, and is mediated by a relatively simple neural circuit.

Also, the startle response is time-locked to stimulus onset, and can be measured noninvasively. A wealth of developmental and comparative data exists, illustrating the generalizability of the startle response across studies, subjects, and species.

Landis and Hunt (1939) found that the eyeblink is the first component of the startle response to appear, and that this reflex eyeblink is very reliable, resisting habituation. The reflex eyeblink is also a sensitive measure, in that it varies predictably with very small stimulus changes (Davis & Heninger, 1972).

Lesion and electrical stimulation studies in the rat have shown that the acoustic startle response is mediated by a relatively simple neural circuit (Davis, Gendelman, Tischler, & Gendelman, 1982). Auditory input ascends via the auditory nerve and the ventral cochlear nucleus to the nuclei of the lateral lemniscus, which connect to the nucleus reticularis pontis caudalis, and this is the beginning of the motor output component of the startle pathway. Startle is a brainstem reflex that can be found in decerebrate animals (Davis & Gendelman, 1977; Fox, 1979), and in anencephalic infants (W. K. Berg, unpublished data).

Startle has been measured in adult and infant animals and humans, using a variety of techniques. In animal research, the two most common measures are electromyographic (EMG) activity of the flexor muscles of the leg, and the whole-body jerk, as measured by an accelerometer in a rigidly suspended cage. In humans the eyeblink component is assessed, either by measuring the movement of the eyelid with a potentiometer, or by measuring the EMG activity of the orbicularis oculi, the muscle responsible for the eyeblink. The advantage of using the eyeblink

component of startle in the human is that it has a lower threshold than either flexor EMG or whole-body jerk, so minimally-startling stimuli can be used. The EMG measure may be preferred to lid movement, since EMG activity can be found in the absence of lid movement, whether the eyes are open or closed, making EMG both more sensitive and more versatile than lid movement.

Startle responses can be assessed by the application of two different paradigms. First, the direct effects of stimuli on the startle response can be studied, by varying the eliciting stimuli and measuring the resultant changes in the startle response. Second, the modification of the startle response by a nonstartling stimulus (called a prepulse), occurring before the eliciting stimulus, can be measured. The first technique is aimed at a direct assessment of the startle system, while the second technique uses the startle stimulus as a probe to investigate processing of the prepulse.

The degree to which a stimulus will elicit startle is affected by several factors. Increasing stimulus rise time results in higher startle thresholds, in both rats (Fleshler, 1965) and human adults (Berg, 1973). Increasing rise time also results in smaller blinks for suprathreshold stimuli in human adults (Blumenthal & Berg, 1984) and infants (Blumenthal & Berg, 1982). Increasing stimulus intensity yields larger responses in adults (Blumenthal & Berg, 1984) and in rats (Marsh, Hoffman, & Stitt, 1973). Increasing stimulus duration up to 8 ms, but not beyond, yields larger responses in rats (Marsh, Hoffman, & Stitt, 1973), and this critical duration decreases as stimulus intensity increases. In human adults, the critical duration is longer than it is in rats. Berg (1973) increased stimulus duration up to 32

ms, and found a continuing increase in response amplitude. Yamada (1983) found that response amplitude increased as stimulus duration increased to 30-50 ms, but not beyond. This illustrates a critical duration for human adults which is considerably higher than that for rats. The critical duration for Infants has not previously been reported.

In rats, increasing the interval between two brief (1 ms) pulses to 3 ms (onset-to-onset) results in larger responses, with a return to the level of a single 1 ms pulse when interpulse interval is increased to 6 ms (Marsh, Hoffman, & Stitt, 1973). The increase in responding as interpulse interval is increased to 3 ms may be due to a reduction of neural refractoriness and more complete peripheral recovery. At interpulse intervals greater than 6 ms, the second pulse appears to have no effect, illustrating a critical interval for summation of transients of 6 ms in rats.

The startle modification technique uses the startle stimulus as a probe, and can be used to assess stimulus processing in several modalities. This method involves the presentation of the stimulus to be assessed, the prepulse, some brief time before the startle stimulus. Depending on the stimulus parameters of the prepulse, the startle response can be inhibited or facilitated in several ways. The amount of modification is wholly dependent upon the parameters of the prepulse, with the startle-eliciting stimulus having no effect on the modification (Stitt, Hoffman, & Marsh, 1976).

The time between onset of the prepulse and onset of the startle pulse is called lead time, and this is an important factor in determining modification effects. At lead times of 10 ms or less in the

rat, or 30 ms or less in the human, a prepulse above detection threshold will cause a decrease in the latency of the subsequent startle response (Hoffman & Ison, 1980). At lead times of 30-240 ms in both rats and humans, startle amplitude is reduced by the prepulse (Hoffman & Ison, 1980). The optimal lead time, where the amount of inhibition of amplitude is maximal, is about 120 ms in adults. If lead time is equal, prepulses which remain on throughout the lead time are no more effective than those which have a duration of 20 ms (Graham & Murray, 1977). However, as the duration of transient prepulses increases, more amplitude inhibition is found. This may be because the onset and offset of the transient prepulse become more independent as they are separated in time, so their combined effect is increased (Harbin & Berg, 1984). *

In infants, the transient-sensitive system is believed to be immature (Graham, Strock, & Zeigler, 1981). For maximal inhibition of startle amplitude by a transient prepulse in 6-to-9-week-olds, lead time must be 225 ms, as compared with 120 ms in adults. More intense prepulses are required with these infants, and the prepulses must be

* If a brief, transient stimulus occurs at a very long lead time, it will have no effect, unless attention is directed to the prepulse (as indicated by heart rate deceleration) (Bohlin, Graham, Silverstein, & Hackley, 1981). If attention is directed towards the sensory modality in which the startle stimulus occurs, the startle response will be facilitated; if attention is directed away from the startled modality, inhibition occurs. The attentional effect can combine with the effect of a sustained prepulse, resulting in more facilitation than to either effect alone (Bohlin, Graham, Silverstein, & Hackley, 1981). The reason for this attentional effect may be that heart deceleration, or orienting, may cause an enhancement of stimulus input so that the effectiveness of a startle stimulus occurring during orienting to a prepulse is increased (Lacey & Lacey, 1974).

slightly longer (25 - 30 ms in infants, 20 ms in adults) in order to be effective (Zeigler, Strock, & Graham, 1979). Even at optimal lead times, inhibition is less marked in infants than in adults (Graham, Strock, & Zeigler, 1981). Since startle inhibition is argued to be a function of transient system activity, these findings suggest that the temporal summation of transients is immature in infants.

At very long lead times (2-4 sec) a prepulse which stays on throughout the lead time (sustained prepulse) can cause an increase in startle amplitude in adults and infants, but optimal lead time is longer for infants (4 sec) than for adults (2 sec). However, the degree of facilitation is similar at the two ages, supporting the belief that the sustained processing system is relatively mature in infancy (Graham, Strock, & Zeigler, 1981). In rats, startle inhibition and facilitation have been investigated at the neurochemical level and appear to be due to the activation of different receptor sites. The receptors responsible for facilitation of startle appear to mature earlier than those responsible for inhibition (Gallager, Kehne, Wakeman, & Davis, 1983). If an analogous arrangement exists in the human, developmental differences in startle modification may be expected.

Immaturity of the transient system has been proposed, based on evidence using the startle modification paradigm (Graham, Strock, Zeigler, 1981). A more direct assessment of the transient system may be possible by using the startle elicitation paradigm, investigating stimulus effects on the startle response directly, rather than its modification by a prepulse (Dykman & Ison, 1979). Also, if transient system immaturity is believed to exist, it may be most apparent in

newborns, so this age group, rather than older infants, should be studied.

In the present study, the temporal summation of transient and sustained stimuli was assessed in human adults and newborns, using the startle elicitation technique. The stimuli used were either single stimuli, varying in duration (3-100 ms), or pairs of brief (3 ms) stimuli, with onset-to-onset intervals analogous to the duration of the single stimuli. Since peripheral recovery requires more than 3 ms (Green, 1973), the offset of very brief pulses may have a minimal effect, so the paired stimuli were treated as two transients rather than four. These stimuli were used to assess transient system activity directly.

The single stimuli longer than 3 ms included transients (at onset and offset) and a steady-state portion (between onset and offset) so that responding to these stimuli could be contributed to by both transient and sustained system activity. The contribution of the sustained system could be assessed in three ways, all of which involve the assumption that the onset of single stimuli has an effect equivalent to that of the first pulse in a pair of brief pulses, that is, transient system activity. The assessment of sustained system activity differs in how the stimulus components following onset (i.e. steady-state portion and offset) affect responding.

Stimulus offset may be assumed to have no effect on the startle response, if startle is a function of a sufficient increase in stimulus intensity occurring within a sufficiently brief time, as Graham (1975) states. Therefore, subtracting the response to a 3 ms pulse from that to a longer pulse (subtraction of onset transient) would yield the

effect of the steady-state portion of the stimulus. However, the influence of stimulus offset on startle has not been shown to be irrelevant, so ignoring this possible effect may result in an overestimation of sustained system activity (since some of the response remaining may be due to transient system activity).

A second way to infer sustained system activity is to subtract the response to a pair of transients from the response to an analogous single stimulus. This assumes that offset is as powerful a transient as onset, and that startle is determined by sufficient stimulus change in either direction. With this method, sustained system activity will be underestimated if offset is not as effective a transient as onset (since transient system activity will be overestimated).

Since the effect of stimulus offset has not been quantified, it may be useful to consider the situation where the effect of the offset transient is greater than zero but less than that of the onset (or the 3 ms pulse). If a single stimulus is no more effective than an analogous pair of stimuli, it is assumed that the steady-state portion and offset of the single stimulus are no more effective than the second pulse in a pair. The degree to which single stimuli are more effective than paired stimuli indicates sustained system activity, though the full effect cannot be ascertained unless offset transient effects can be determined. However, if stimulus duration increases and responding does not change, sustained system activity may have a minimal contribution. This does not necessarily mean that sustained activity is not occurring, it just means that this activity is not contributing much to the response. When both transient system activity and sustained system activity are present, their contributions to the response may be

unequal. If the activation of the more efficient system is decreased, the activity of the other system may become more apparent. The only case in which the contribution of sustained system activity would be ambiguous is that for paired stimuli which produce larger responses than single stimuli. The lower responding to single stimuli could be due to either reduced sustained system activity or to reduced transient system activity at onset.

To assess the activity of the sustained system more directly, research using stimuli with minimal transients (long rise and fall times) is needed. The effects of stimulus onset alone could be examined with fast-rising, slow-falling stimuli, so that no offset transient occurs. Stimulus offset effects could be isolated with slow-rising, fast-falling stimuli, to minimize the onset transient. These avenues of research are suggested to explore the sustained processing system more fully.

CHAPTER 11 EXPERIMENT 1

Method

Subjects

Subjects were 16 adults, 6 males and 10 females, with a mean age of 20 years (range=18 to 27 years), selected from a university undergraduate subject pool, who reported no history of hearing loss and no use of medications on the day of testing.

Stimuli

Broadband noise bursts (20Hz-20kHz), at 95 dB(A), with a rise-fall time of less than 0.1 ms were used. Seven of the stimuli varied in duration (3, 20, 35, 50, 65, 80, and 100 ms), and six others consisted of pairs of 3 ms pulses at intervals analogous to the durations used (20, 35, 50, 65, 80, and 100 ms, measured from onset to onset). Intertrial interval ranged from 25-35 sec, averaging 30 sec.

Apparatus

Stimuli were produced by a Grason-Stadler 455C noise generator gated through an Iconix electronic switch and a Sansui AU517 amplifier, and presented through a JBL Decade 26 loudspeaker, located approximately 1.5 m in front of the subjects. Stimulus intensity was calibrated using a General Radio 1551C sound level meter and monitored with a Hewlett-Packard 400E AC voltmeter.

Peri-orbital electromyographic (EMG) responses were collected using miniature Beckman biopotential electrodes (Ag/AgCl) filled with Synapse conducting paste. The EMG signal was amplified by a Coulbourn Hi-Gain Bioamplifier/Coupler, with filters passing frequencies of 90-250 Hz, and a gain of 63,000. The signal was then integrated with a Coulbourn Contour Following Integrator at a time constant of 80 ms (Integrated EMG). * The integrated EMG was then recorded on a Beckman R411 polygraph, as well as being digitally sampled (10 bit accuracy) by a PDP-8 computer every millisecond for 250 ms after stimulus onset.

Procedure

The experimenter explained the procedure and the subject was asked to read and sign an informed consent statement, and to fill out a background questionnaire. The experimenter then cleaned the area just below the left eye with a cotton swab soaked in alcohol, and two electrodes were attached, one below the center of the eye, and the other immediately temporal to the first, as close to the orbital ridge as possible without impairing eye movement. The subject was then seated in the testing room and asked to move as little as possible, especially the eyes and head. Data were used only from trials on which an experimenter, watching the subject on closed circuit television, judged the eyes to be open. If a stimulus was presented when the eyes were closed, or during movement of the head or eyes, the trial was rejected

* The integrator time constant was determined by calibration, not by the setting on the integrator itself. It was found that the time constant settings of two integrators of the same model varied widely, so the only reliable way to determine the actual time constant was to calibrate each separately.

by an experimenter blind to stimulus conditions. An average of 7.5 percent of the trials were rejected for each subject, and rejection was not more likely for one stimulus condition than for any other. A 13×13 Latin square was used to determine stimulus order, with the row of entry into the square being randomly determined. A session was terminated when six potentially scorable responses in each stimulus condition were obtained.

Data Analysis

Response amplitude was measured as the difference between response onset and peak. Response onset was judged only during the window between 20 and 100 ms after stimulus onset. Initiation of a response was judged on the basis of a monotonic increase in EMG that continued for at least 20 ms. Onset latency was then judged as the point where this increase exceeded the random variability in the 20 ms prior to this increase. The peak of the response was the first point following onset where the slope of the integrated EMG signal equalled or passed through 0, when this was followed by at least 10 ms with no further slope reversal. Response latency was measured as the time from stimulus onset to response onset.

Response probability was measured as the degree to which responses actually occurred when subject variables were optimal (i.e. eyes open, no head movement). If the integrated EMG signal during the response window did not deviate beyond the random noise present prior to the onset window, a failure to respond was recorded. Due to the considerable sensitivity of the computer sampling and amplifier, the degree to which very small responses were not detected was minimal.

The response parameter most often reported by researchers in this area is average magnitude, which is calculated from trials on which a response could have been recorded, whether a response actually occurred or not (e.g. Graham & Murray, 1977). Magnitude changes can be due to changes in either response probability or amplitude (Prokasy & Ebel, 1967), and these two may be partially independent measures of startle responding (Blumenthal & Berg, in press). Therefore, the present study examined response amplitude and probability separately. For each subject, response amplitude and latency were averaged across trials for each condition. ANOVAs including stimulus type (single or paired) and time (duration or interval in msec) as within-subject variables were conducted. To balance the analyses, data from the 3 ms single stimulus condition were duplicated for use in paired stimulus comparisons, as a substitute for a pair of pulses at an interval of 0 ms.

Results

Amplitude

The effect of increasing stimulus duration or interpulse interval on response amplitude differed, as illustrated by a significant stimulus type by time interaction, $F(6,90)=8.88$, $p<.001$ (see Figure 1). Increasing stimulus duration to 50 ms, but not beyond, resulted in larger responses, as shown by significant linear, $F(1,15)=18.23$, $p<.001$, and quadratic, $F(1,15)=15.37$, $p<.001$, trends. Responses were larger at 20 than at 3 ms duration, $t(15)=4.13$, $p<.001$, and larger at 50 than at 35 ms duration, $t(15)=2.64$, $p<.025$. No other pairwise comparisons reached significance, indicating that increasing duration

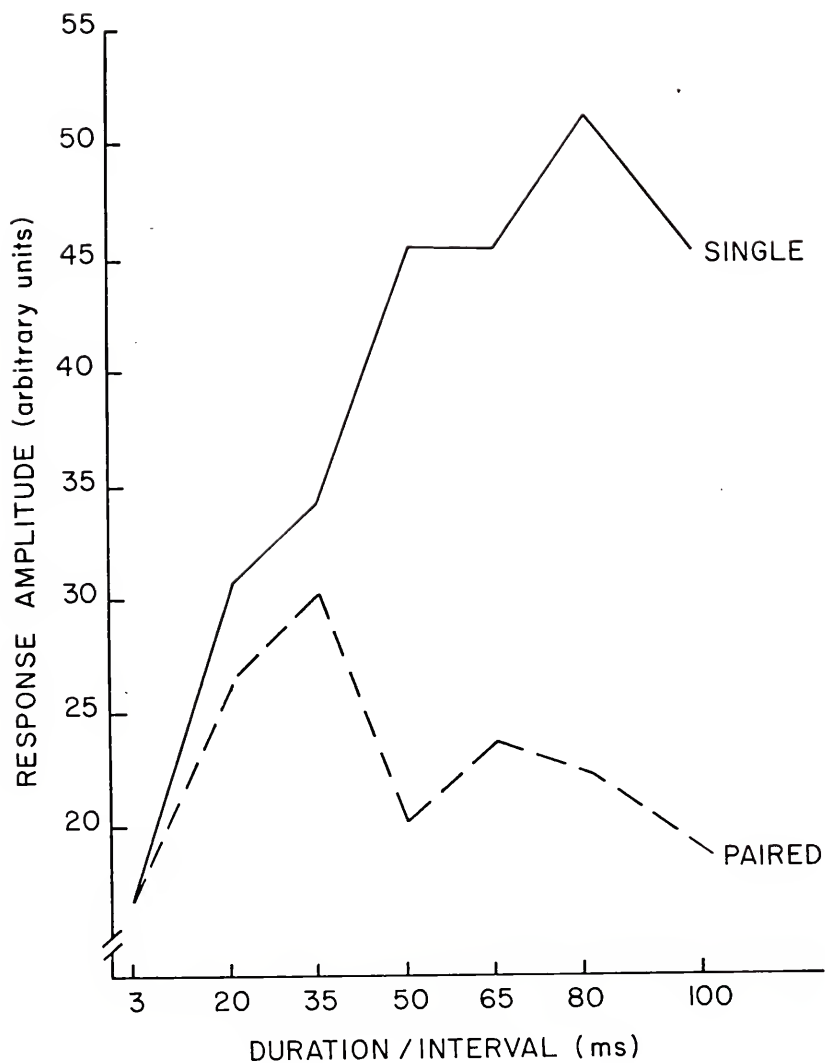


Figure 1. Adult response amplitude as a function of time for single and paired stimuli.

above 50 ms had no significant effect. Increasing Interpulse Interval to 35 ms, but not beyond, resulted in larger responses, yielding a significant quadratic trend, $E(1,15)=5.61$, $p<.05$, and a marginally significant cubic trend, $E(1,15)=4.46$, $p<.052$. Responses were larger for a pair of pulses at 20 ms interval than for a single 3 ms pulse, $t(15)=2.20$, $p<.05$. Increasing interval from 3 to 35 ms resulted in larger responses, $t(15)=2.85$, $p<.025$, but responses were not significantly larger at 35 than at 20 ms interval. At intervals of 50 ms or more, responses were not significantly larger than for a single 3 ms pulse. Up to 35 ms, a single stimulus was not significantly more effective than a pair of transients, showing that, even with much less total energy, a second transient was as effective as the sustained portion and the offset of a single stimulus. This indicates an asymmetrical input of transient and sustained stimuli to the startle system, with transient input being more effective than sustained input, up to 35 ms. Above 35 ms, the second transient had little effect, whereas the sustained portion of the stimulus increased in effectiveness, reaching asymptote at 50 ms.

Probability

For response probability, the effect of increasing stimulus duration or Interpulse Interval also differed, as illustrated by a significant stimulus type by time interaction, $E(6,90)=5.34$, $p<.001$ (see Figure 2). A linear effect of duration appeared, $E(1,15)=13.29$, $p<.01$, and this was due mainly to increasing duration from 3 to 20 ms, $t(15)=2.22$, $p<.05$. In fact, if the 3 ms data were excluded from the analysis, no significant duration effect was found, $E(1,15)=2.12$. For

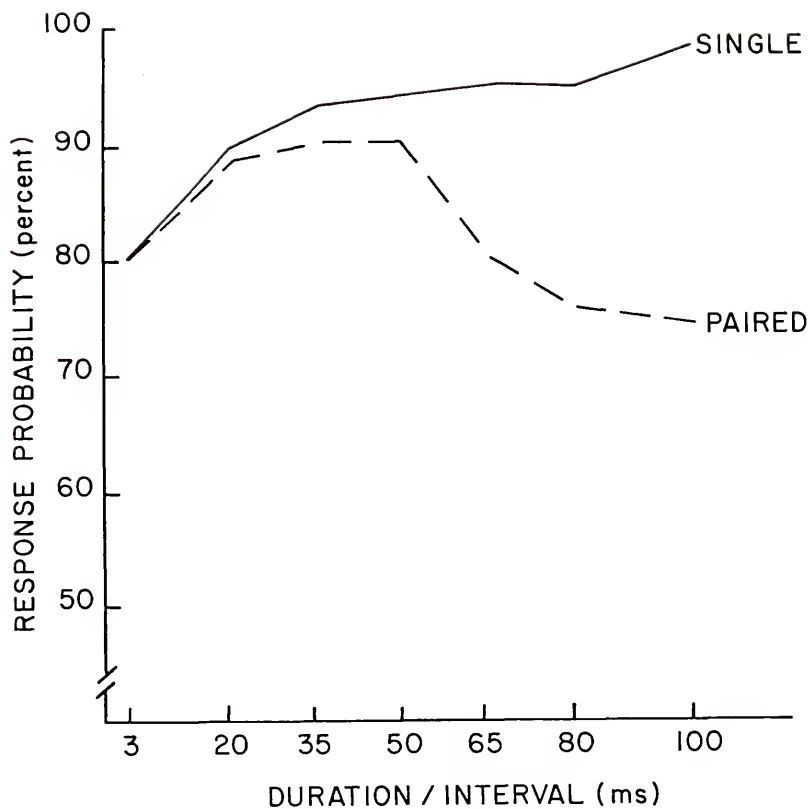


Figure 2. Adult response probability as a function of time for single and paired stimuli.

paired stimuli, a quadratic trend appeared, $E(1,15)=6.16$, $p<.025$. Increasing interpulse interval to 50 ms had no further effect. At longer intervals, the contribution of the second pulse disappeared, with probability at intervals of 65, 80, and 100 ms not significantly different from that for a single 3 ms pulse. Up to 50 ms, the difference in probability between single and paired stimuli was not significant, illustrating a dominant transient contribution. When the second transient was no longer effective, the sustained portion of the stimulus maintained a high response probability. However, the interpretation of these probability data may be influenced by a ceiling effect for single stimuli.

Latency

Response latency was affected by increasing stimulus duration or interpulse interval, $E(6,90)=2.22$, $p<.05$, and stimulus type had a significant effect, $E(1,15)=10.40$, $p<.01$, but the stimulus type by time interaction was not significant (see Figure 3). For single stimuli, increasing duration had an effect on latency, $E(6,90)=4.43$, $p<.001$, but this was due to the increase from 3 to 20 ms only, since, if the 3 ms data were not included in the analysis, no duration effect was found ($E(5,75)=0.64$). For paired stimuli, increasing interpulse interval had no effect on response latency.

Discussion

The findings of Experiment 1 show that temporal summation of transient acoustic input dominates that of sustained input, in adults. Transients occurring within a window of 35-50 ms summate, and sustained

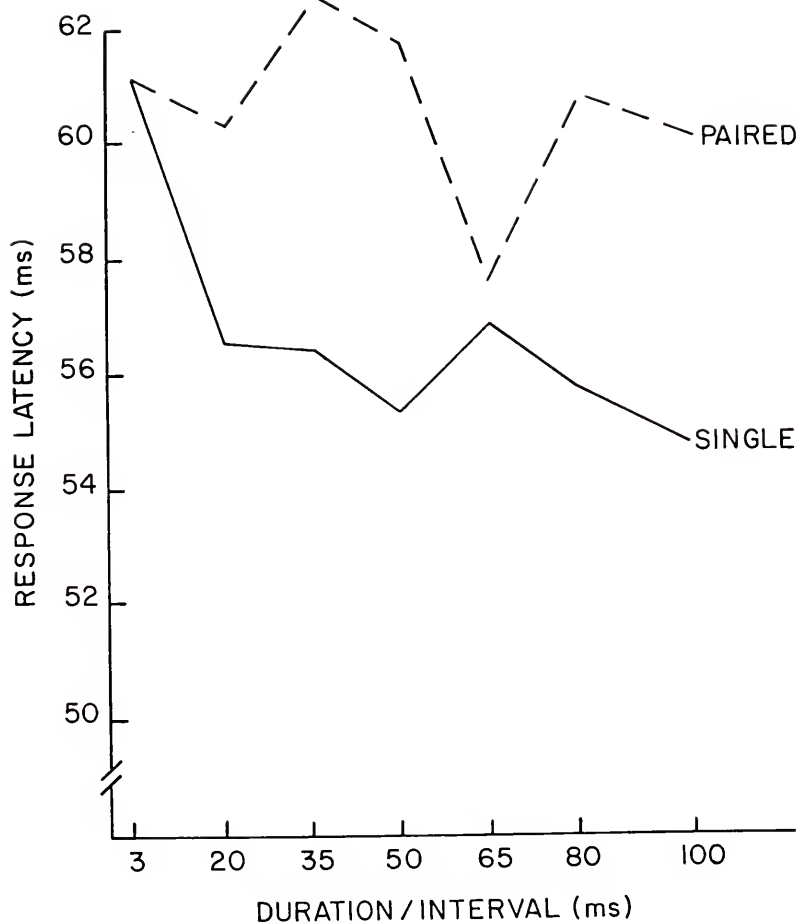


Figure 3. Adult response latency as a function of time for single and paired stimuli.

summation adds little which cannot be explained by transient summation in this range. Beyond this window, transient summation does not occur, and the contribution of sustained summation becomes apparent. Also, these differential summation effects are reflected by startle response amplitude, probability, and latency in different ways.

For response amplitude the summation window for transients is 35-50 ms, and the time between transients has a slight, but not significant, effect on the response. As interpulse interval within the window increases, a slight increase in response amplitude may be explained by forward masking, which suggests that the first pulse decreases the effectiveness of the second. As the interpulse interval increases the amount of masking decreases (Raab, 1961), so that responding at the 20 and 35 ms intervals may differ due to a reduction in responding at the 20 ms interval, but not at the 35 ms interval (or, at least, not as great a reduction). If forward masking is present, its influence is not great, possibly due to the brief duration of the first pulse (Zwislöcki, 1978). Also, this marginal masking effect was found for response amplitude, but not for response probability.

For response probability, the summation window extends to 50 ms, and the effect of the second transient is not influenced by where in this window it occurs, above 20 ms. For response latency, the second transient had no apparent effect at any of the intervals used. It may be the case that the temporal summation window for transients is narrower than 20 ms, so that the second pulse always occurred outside the window, and this prediction may be supported by future research. For sustained summation, 20 ms is adequate, but the window may be less than this.

After the transient summation window has been exceeded, sustained summation continues to occur, either increasing responding or maintaining elevated responding after the effect of the second transient has disappeared. This peaks at 50 ms for response amplitude, and at 20 ms for response latency. For response probability, the peak of the sustained summation function is difficult to specify due to the presence of a ceiling effect at high probabilities, but this peak could not exceed the peak response latency (approximately 65 ms). Also, the extent to which the second pulse in a pair elicited a response when the first pulse failed to do so was minimal (less than 10 instances for all subjects combined). This means that the second pulse alone is not effective in eliciting responding.

The temporal summation of transient stimuli peaked at 35 ms for response amplitude and 50 ms for response probability. Within these ranges, the contribution of the sustained portion of a stimulus was no greater than that of the second brief transient. Beyond these ranges, the second stimulus in a pulse pair had little or no effect, but responding was maintained by the sustained portion of a single stimulus. A second experiment was conducted, to investigate these temporal summation properties in greater detail.

CHAPTER III EXPERIMENT 2

Introduction

The data of Experiment 1 suggest that the temporal summation window for transient stimuli is 35-50 ms for response amplitude and probability, and less than 20 ms for response latency. To more accurately assess responding in the critical range of 35-50 ms, a second experiment was conducted, in which stimulus duration and interpulse intervals in the 30-55 ms range were varied in 5 ms steps.

Method

Subjects

Subjects were 12 university students, 6 males and 6 females, with an average age of 22 years (range=18 to 29), selected in the same way as in Experiment 1.

Stimuli, Apparatus, Procedure, and Data Analysis

These were identical to those used in Experiment 1, except that stimulus durations were 3, 30, 35, 40, 45, 50, and 55 ms, with analogous interpulse intervals for paired (3 ms) stimuli.

Results

Amplitude

Response amplitude was affected by increasing stimulus duration or interstimulus interval, $E(6,66) = 3.70$, $p < .005$, and stimulus type had a significant effect, $E(1,11) = 29.71$, $p < .001$, but the two variables

did not interact (see Figure 4). For single stimuli, a significant linear trend for duration was found, $E(1,11) = 9.70$, $p < .01$. A single 30 ms stimulus was more effective than a 3 ms stimulus, $t(11) = 2.86$, $p < .025$, but further increases in stimulus duration were not significantly more effective than a 30 ms stimulus. For paired stimuli, a significant quadratic time trend was found, $E(1,11) = 6.81$, $p < .025$. Pairs of pulses at intervals of 35, 40, and 45 ms were slightly, but not significantly, more effective than a single 3 ms stimulus ($t(11) = 2.09$, $p < .06$; $t(11) = 1.98$, $p < .08$; $t(11) = 2.02$, $p < .07$, for 35, 40, and 45 ms, respectively). At 50 and 55 ms intervals, pairs of pulses were clearly no more effective than single 3 ms stimuli. Single stimuli were significantly more effective than paired stimuli at 50 ms, $t(11) = 3.44$, $p < .01$, but not below.

Probability

The effect of increasing stimulus duration or intersimulus interval differed for response probability, as illustrated by a significant stimulus type by time interaction, $E(6,66) = 2.27$, $p < .05$ (see Figure 5). For single stimuli, a linear trend for duration was found, $E(1,11) = 7.53$, $p < .025$. A 30-ms duration stimulus was more effective than a 3 ms stimulus, $t(11) = 2.40$, $p < .05$, but no significant difference was found between a single 3 ms pulse and pairs of pulses at all other intervals tested. For paired stimuli, a significant quadratic interval trend was found, $E(1,11) = 5.64$, $p < .05$. A pair of pulses 30 ms apart were more effective than a single 3 ms stimulus, $t(11) = 2.52$, $p < .05$, but further increases in interstimulus interval had no significant effect. A single stimulus was more

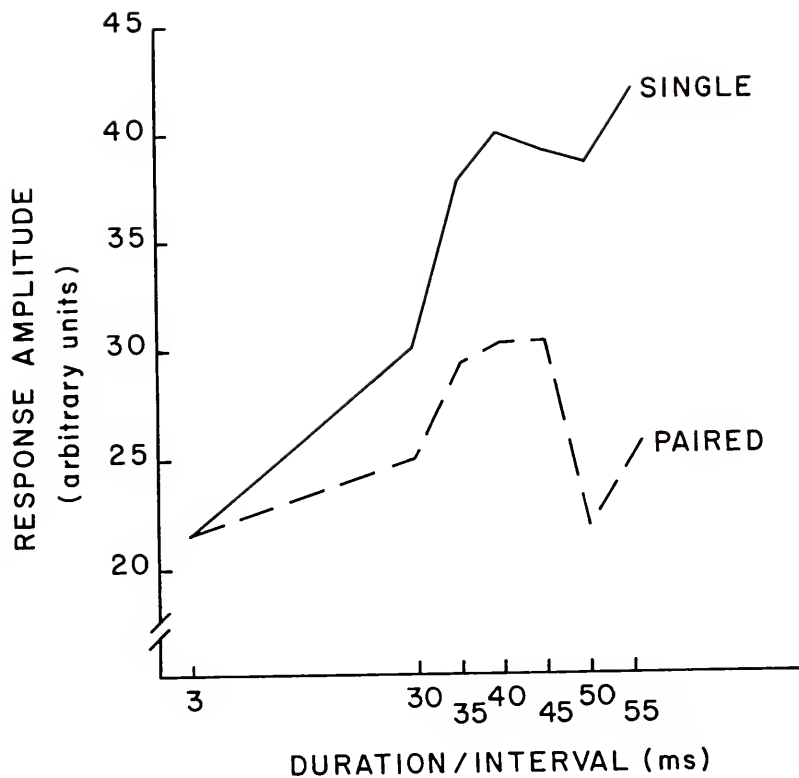


Figure 4. Adult response amplitude as a function of time for single and paired stimuli.

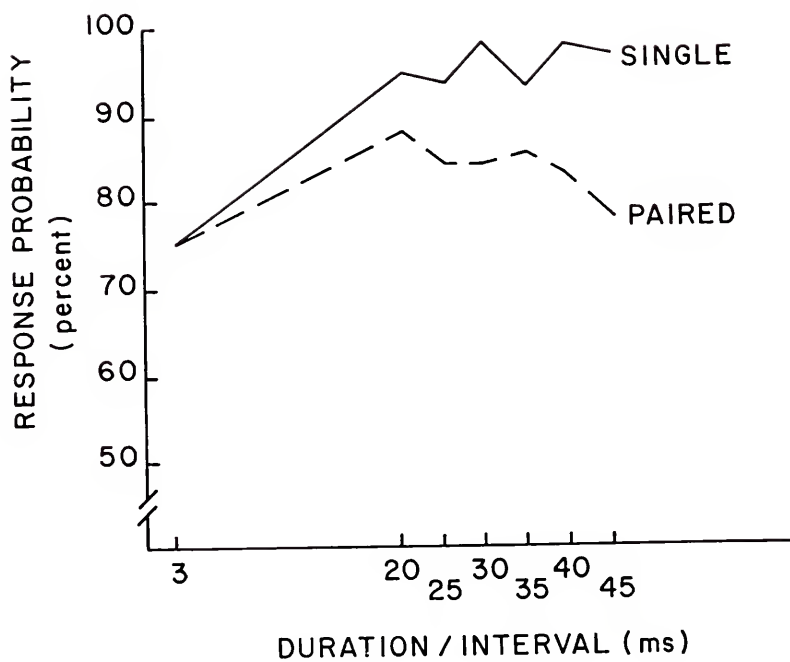


Figure 5. Adult response probability as a function of time for single and paired stimuli.

effective than an analogous pair of stimuli at 40, 50, and 55 ms (\pm (11) = 2.32, 2.28, and 2.54, respectively, $p < .05$).

Latency

A significant stimulus type by time interaction was found for response latency, $F(6,66) = 2.54$, $p < .05$ (see Figure 6). For single stimuli, the overall time effect was not significant, but latency was lower for 40 ms stimuli than for 3 ms stimuli, \pm (11) = 3.39, $p < .01$. For paired stimuli, a linear effect of interstimulus interval was found, $F(1,11) = 14.65$, $p < .005$. Increasing interval from 30 to 50 ms resulted in a significant increase in response latency, \pm (11) = 2.75, $p < .025$, but no other comparisons of paired stimuli were significant. Latencies for single stimuli were significantly lower than those for paired stimuli, at each interval tested.

Discussion

For response amplitude, increasing stimulus duration to 30-55 ms resulted in larger responses, as illustrated by a significant linear trend for duration. Increasing interstimulus interval for paired stimuli resulted in larger responses up to 40 ms, then a reduction in response amplitude, as shown by the significant quadratic function for paired stimuli. Single stimuli were not significantly more effective than paired stimuli below 50 ms. In Experiment 2, the two functions diverged between 35 and 50 ms, just as they did in Experiment 1. The fact that the response amplitude functions are so similar in the two experiments suggests that these findings are reliable. Up to 35 ms, the transient aspects of the stimulus seem almost as effective as the

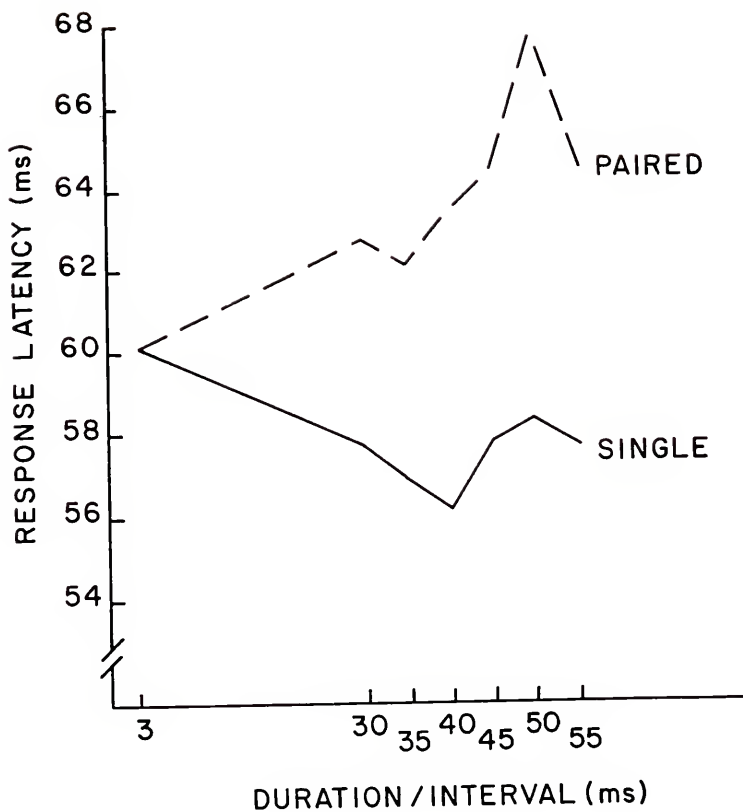


Figure 6. Adult response latency as a function of time for single and paired stimuli.

sustained aspects in determining response amplitude.

In Experiment 1, it was shown that temporal summation for response probability may peak below 20 ms, and this was supported in Experiment 2. Increasing stimulus duration from 3 to 30 ms resulted in increased response probability, with further increases to 55 ms having no greater effect. A pair of stimuli 30 ms apart were more effective than a single 3 ms pulse but further interval increases were not effective. Paired pulses were as effective as single pulses up to 45 ms, above which the effect of the second pulse in the pair tended to decrease. This parallels the finding in Experiment 1 that transient summation is as effective as sustained summation up to 50 ms.

The response latency data of Experiment 2 are also similar to those of Experiment 1, but not as clearly as were the amplitude and probability data. Latency was lower for single than for paired stimuli, in all cases. However, where the latency effect for single stimuli peaked at 20 ms in Experiment 1, it peaked at 40 ms in Experiment 2. Also, where no effect of latency was found for paired stimuli in Experiment 1, longer latency was found at 50 than at 30 ms intervals in Experiment 2. The reason for these latency differences in the two experiments is not clear, but these data suggest that latency may be a less reliable measure of startle activity than either response amplitude or probability.

Experiments 1 and 2 show that the temporal summation of acoustic stimuli occurs in different ways for transient and sustained stimuli, and that this differential summation is reflected in different ways by startle amplitude, probability, and latency. For response amplitude, transient summation dominates for 40 ms, and sustained summation adds

little during this time. Beyond the transient summation window, sustained summation continues to increase response amplitude for a brief time (<20 ms). For response probability, summation of transients peaks at less than 20 ms, and continues to 50 ms, with minimal contribution by sustained summation in this period. Above 50 ms, sustained summation maintains elevated probability while the effect of a second transient disappears. The probability and amplitude functions are similar in that the temporal summation window for transients is not more than 50 ms in both cases, but this summation seems to peak earlier for probability than for amplitude. Response latency appears to reflect summation properties similar to those shown by probability, but in a less reliable fashion.

Experiments 1 and 2 illustrate the fact that the startle elicitation paradigm provides an effective tool for comparing transient and sustained system activity. Therefore, it would be of interest to apply this paradigm to infant subjects, since Graham, Anthony, & Zeigler (1983) hypothesize that the transient system is relatively immature when compared to the sustained system in infants. Experiment 3 measured startle amplitude, probability, and latency to stimuli analogous to those used in Experiments 1 and 2. If transient immaturity exists, these measures should show differences between infants and adults.

CHAPTER IV EXPERIMENT 3

Method

Subjects

All subjects were apparently healthy newborns, with no significant problems or complications, and were the result of spontaneous vaginal delivery at Shands Hospital in Gainesville, Florida. Data from 4 of 24 subjects tested were not used, due to a failure to respond to at least two trials at each stimulus condition. For the 20 remaining infants, average age was 23 hours (range=7-36 h), average gestational age by maturity rating was 39.75 weeks (range=37-42 wk), average 5 minute Apgar (1953) score was 8.9 (range=8-10), and average birthweight was 3350 gm (range=2640-4220 gm). Testing began an average of 1 hour 10 minutes after the last feeding (range= 30 min- 3 h 30 min). Local anaesthetic was administered to 11 mothers during delivery, with no anaesthetic in the remaining 9 cases.

Apparatus

Stimuli were produced by a Grason-Stadler 455C noise generator, gated through a Coulbourn electronic switch and a Dynaco Stereo 120 amplifier, and presented through a JBL Decade 26 loudspeaker, located 1 m in front of the subjects. Sound levels were checked before each session, using a General Radio 1551C sound level meter and a Simpson 260 voltmeter. The EMG signal was amplified and integrated in the same way as in Experiment 1, except for some variation in Bioamplifier gain

settings. This signal was sampled by an Apple II Plus computer (12 bit accuracy) every millisecond for 250 ms and corrected for gain variations. EKG was recorded on a Teac A-2300SX tape recorder, and on a Narco DMP-4B Physiograph. Respiration was recorded using a Parks Electronics strain gauge and a Parks Electronics Model 270 plethysmograph, and this signal was also displayed on the Narco Physiograph.

Stimuli

Stimuli were broadband noise bursts (20Hz-20 KHz) at 100 dB(A) with fast (< 0.1 ms) rise and fall times. Pilot data showed that 95 dB(A) stimuli (the intensity used in Experiments 1 and 2) did not reliably elicit responding at 3 ms duration. Five of the stimuli varied in duration (3, 20, 35, 50, and 100 ms), and the other four were pairs of 3 ms pulses at onset-to-onset intervals of 20, 35, 50, and 100 ms. Interstimulus interval ranged from 20-60 ms.

Procedure

Each subject was placed supine in a crib in the testing chamber, and the respiration strain gauge was attached laterally across the abdomen, just above the navel. EKG electrodes were attached in a modified Lead II configuration. The area just below the left eye was then cleaned with a cotton swab soaked in alcohol, and the EMG electrodes were attached, one just below the center of the eye and the other immediately temporal to the first, as close to the orbital ridge as possible. Stimulus presentation was controlled by an experimenter, sitting beside the loudspeaker, who also recorded the state of the infant on each trial, using the rating scale of Berg, Berg, and Graham

(1971). These behavioral ratings, along with respiration and EKG measures, were used to determine the state of the infant, and these three measures have been shown to be adequate and reliable indicators of sleep state in young infants (Anders, Emde, & Parmelee, 1971). Only trials during which the infant was judged to be in quiet sleep were included in the analysis. Stimuli were not presented during movement of the head, eyes, or arms, or when the subject's eyes were open. A session was terminated when 9 potentially scorable responses at each stimulus condition were obtained. If the infant changed state the session was halted, and the infant was allowed to return to quiet sleep. If the subject did not reach quiet sleep within an hour, the truncated session was terminated. Stimulus order was determined by a 9x9 Latin square, with the row of entry into the square being randomly determined. Response amplitude, probability, and latency were measured in the same way as in Experiment 1.

Results

Amplitude

A significant effect of stimulus type was found, $E(1,19)=5.13$, $p<.05$, with single stimuli eliciting larger responses than paired stimuli (see Figure 7). A significant time effect was also found, $E(4,76)=6.46$, $p<.001$, but stimulus type and time did not interact. For single stimuli, increasing duration from 3 to 20 ms yielded larger responses, $t(19)=2.09$, $p<.05$, and a further increase from 20 to 35 ms resulted in still larger responses, $t(19)=4.07$, $p<.001$. Increasing stimulus duration above 35 ms had no further effect. For paired stimuli, increasing interpulse interval from 20 to 50 ms resulted in larger responses, $t(19)=2.12$, $p<.05$. Responding to a pair of pulses at

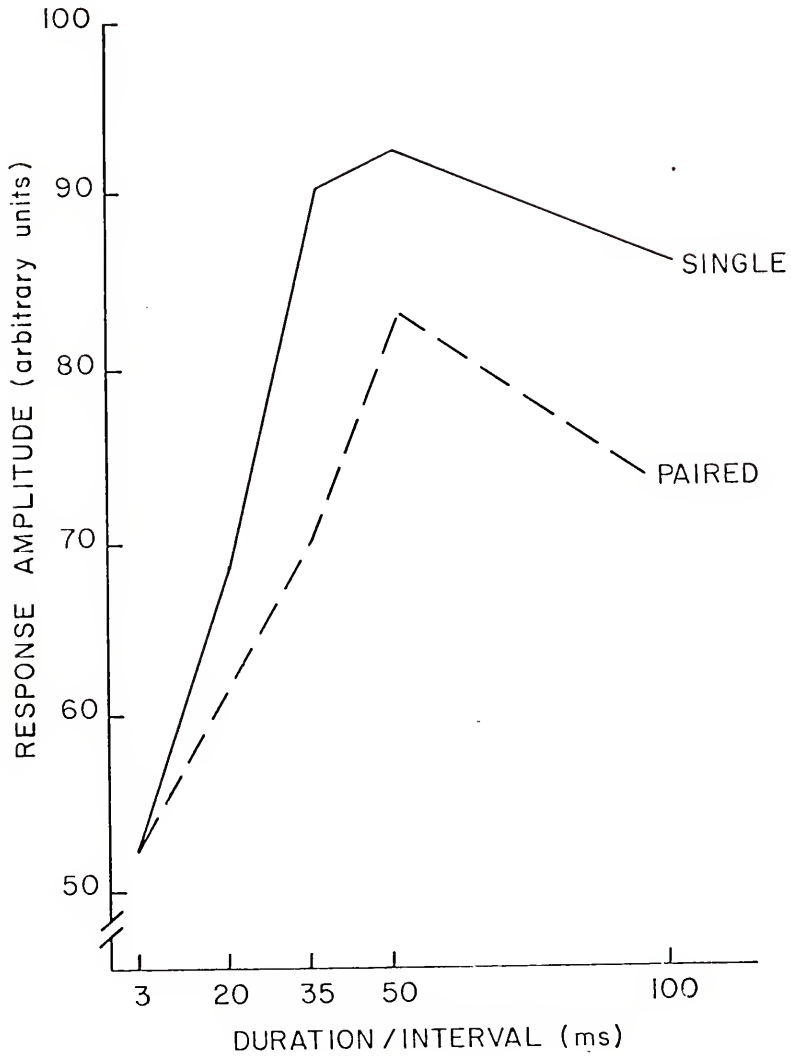


Figure 7. Infant response amplitude as a function of time for single and paired stimuli.

an interval of 100 ms was not significantly different from that to a single pulse at 3 ms duration, suggesting that the second pulse in the pair did not contribute to the response.

A single stimulus 20 ms long was not significantly more effective than a pair of pulses 20 ms apart. At 35 ms, single stimuli were more effective than pairs of pulses, $t(19)=2.47$, $p<.025$, but this advantage was not found at 50 or 100 ms. These findings suggest that a pair of pulses can be nearly as effective as an analogous single stimulus, up to 50 ms. The transient contribution seemed to be dominant in determining responding, with the sustained portion of the stimulus adding little.

Probability

For response probability, an interaction between stimulus type and time was found, $E(4,76)=20.67$, $p<.001$ (see Figure 8). For single stimuli, a quadratic duration trend appeared, $E(1,19)=24.28$, $p<.001$. Response probability increased as stimulus duration was increased from 3 to 20 ms, $t(19)=2.76$, $p<.025$, and from 20 to 35 ms, $t(19)=4.41$, $p<.001$, with duration increases above 35 ms having little effect. For paired stimuli, a quadratic interval effect appeared, $E(1,19)=19.79$, $p<.001$. Probability was not affected by increasing interpulse interval to 50 ms. At 100 ms interval, probability returned to the level found with a single 3 ms pulse, suggesting that the second pulse at 100 ms did not contribute to responding.

A pair of pulses at 20 ms interval was more effective than a single 3 ms pulse, $t(19)=2.82$, $p<.01$, and no less effective than a 20 ms long stimulus. Single stimuli were more effective than paired pulses

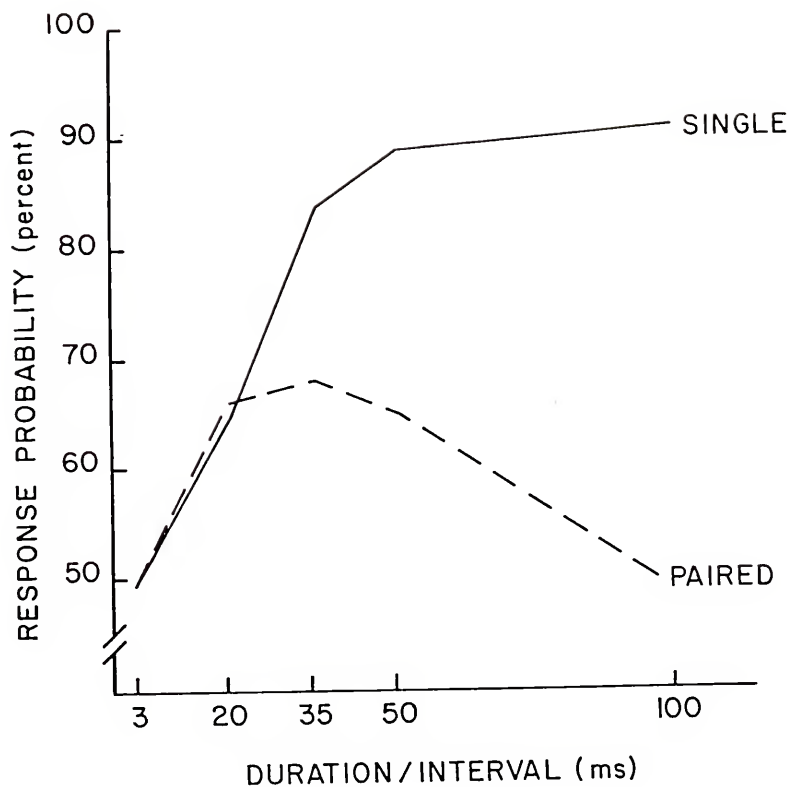


Figure 8. Infant response probability as a function of time for single and paired stimuli.

at 35, 50, and 100 ms, indicating a significant contribution of sustained stimulus attributes above 20 ms.

Latency

A significant effect of stimulus type on response latency was found, $E(1,19)=4.53$, $p<.05$, with latency being slightly longer for paired than for single stimuli (except at 100 ms) (see Figure 9). No significant time effect or stimulus type by time interaction was found. Pairwise comparisons, looking at time comparisons for each stimulus type, and stimulus type comparisons for each time, showed that only the 50 ms single and paired stimuli resulted in different response latency, $t(19)=2.42$, $p<.05$. These data are difficult to interpret, due to the high latency variability, an effect also reported by Zeigler (1978) in 6-to-9-week-old infants.

Discussion

The present study suggests that the temporal summation of auditory stimuli in human newborns follows a different time course for transient and sustained stimuli. Also, startle amplitude, probability, and latency do not reflect this differential summation in the same way.

Response amplitude increases if a second transient is added up to 50 ms after the first. In general, the sustained portion of the stimulus does not seem to contribute much that cannot be accounted for by the transient components of the single stimuli. This suggests that the window for temporal summation of transients is 50 ms for response amplitude, and that transient summation dominates sustained summation in this range.

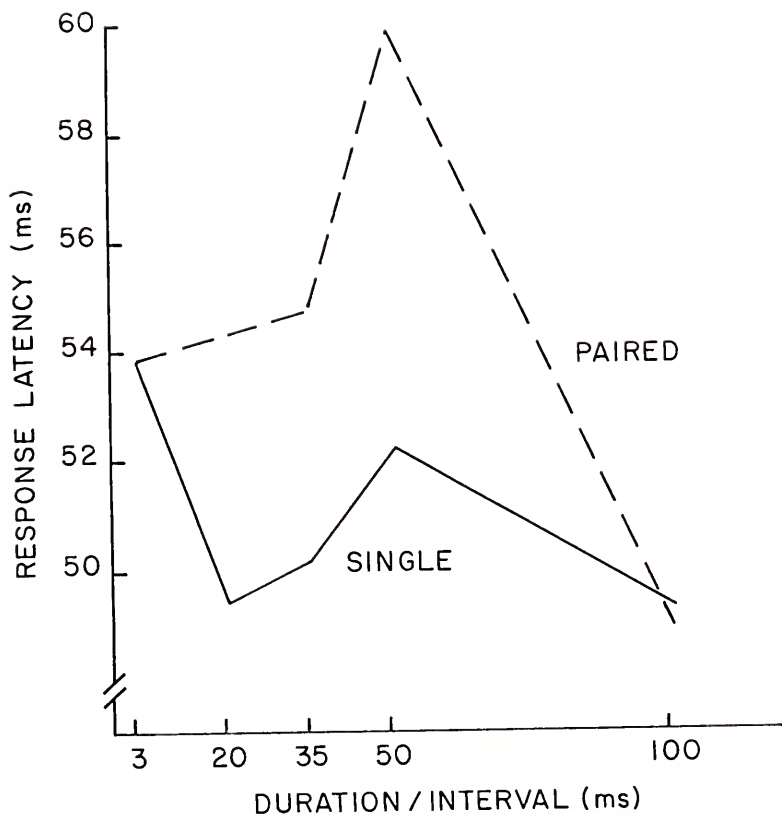


Figure 9. Infant response latency as a function of time for single and paired stimuli.

The fact that response amplitude increases as interpulse interval increases to 50 ms suggests that forward masking may be present, with the first pulse in the pair decreasing the response to the second pulse. As interpulse interval increases, masking decreases (Raab, 1961), allowing the second pulse to contribute more to the response.

The findings for response probability are quite different. Adding a second transient 20-50 ms after the first results in increased likelihood of responding, and the effect of the second transient is not influenced by where it occurs within this window. Sustained summation becomes important above 20 ms, resulting in an increase in probability which asymptotes at 55 ms. This suggests that the window for temporal summation of transients is 20-50 ms, and that sustained summation above 20 ms can add to this, with this sustained contribution reaching its maximum within 35-50 ms of stimulus onset. The effect of the second transient is less pronounced for probability than for response amplitude, so transient and sustained system activity coexist, and both contribute significantly to responding in infants.

CHAPTER V GENERAL DISCUSSION

The startle response is influenced by activity in both the transient and sustained systems, a finding contrary to the hypothesis of Dykman and Ison (1979). These two systems are at least partially independent, with the startle response being the net result of activity in both systems. These experiments show that manipulation of the startle-eliciting stimuli can demonstrate independent influences of transient and sustained system activity. However, the relative contribution to the startle response of these two systems may not be equal, since these results suggest that the transient system is more efficient than the sustained system. As one system becomes dominant over the other, their relative contributions to the response will change.

To find the relative contribution of transient and sustained activity, it is first necessary to calculate the effect of a second 3 ms pulse in a pair if no transient activity were to occur for that pulse. This is accomplished by calculating the slope of the single stimulus function (in units per ms), and adding 3 times this value to the response to a single 3 ms stimulus. If responding to two pulses is simply additive, then 6 ms of stimulation should be equivalent to two 3 ms stimuli. The extent to which the second pulse in a pair affects responding above this predicted level indicates the influence of transient system activity.

The ratio of actual responding to predicted responding (based on linear energy integration) to the second pulse illustrates the relative dominance of transient or sustained system activity. If this ratio is greater than 1.0, transient activity is dominant, since the actual data exceed the predicted values. Ratios less than 1.0 illustrate sustained system dominance.

For response amplitude, the ratios of actual to predicted (linear) response changes due to the presence of a second pulse in a pair are 7.28, 6.13, and 8.72, for Experiments 1, 2, and 3, respectively. For response probability, these ratios are 5.33, 5.87, and 5.23, for Experiments 1, 2, and 3, respectively. Clearly, the effect of the second pulse in a pair is much greater than would be expected if only linear energy integration were occurring. The transient properties of the second pulse enhance responding, and transient system activity dominates sustained system activity when the two occur together.

The response amplitude data suggest that the result of temporal summation of transients is more efficient than that of summation of sustained stimulus attributes, for both neonates and adults. However, the window of temporal summation is narrower in adults (40 ms) than in infants (50 ms). Beyond this window, sustained summation becomes evident. Research using longer durations and intervals is necessary to more accurately specify the transient summation window for neonates.

The infant and adult response probability data suggest that transient summation is maximal within 20 ms, and extends to at least 50 ms, with infant probability being about 20 percent lower than adult probability (see Figure 10), despite the fact that the stimulus was more intense for infants than for adults. The temporal summation of

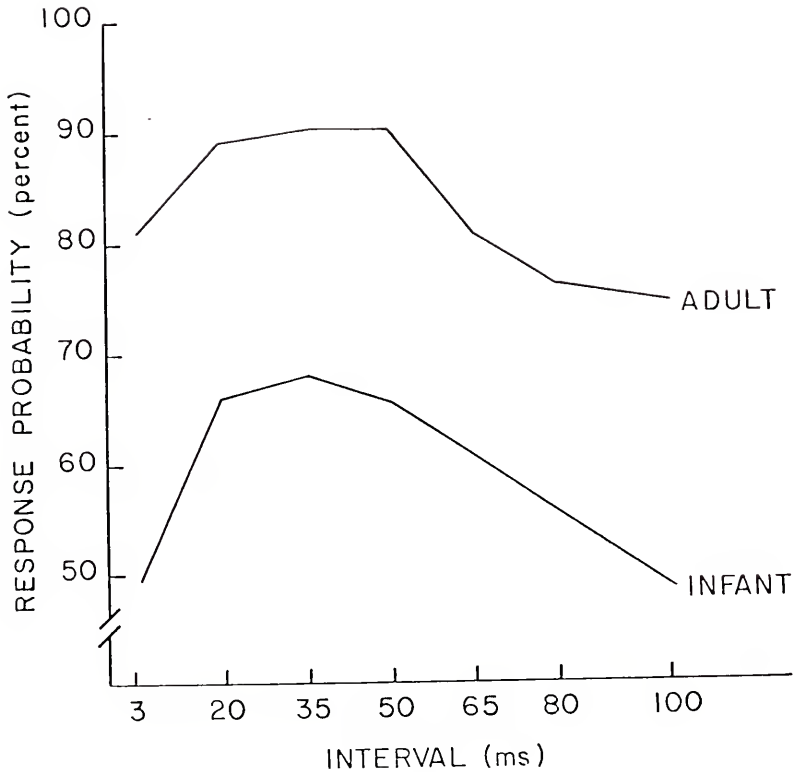


Figure 10. Adult and infant response probability as a function of time for paired stimuli.

transients follows the same time course in adults and neonates, for response probability. For adults, sustained summation contributed little more than could be accounted for by transient summation, and this may have been due to a ceiling effect. In infants, where maximal temporal summation of transients still yielded probabilities below 70 percent, a clear additive effect of sustained summation was found above 20 ms. It may be the case that sustained summation would be more apparent in adults if stimuli which avoid the response probability ceiling were used. When comparing infant and adult probability for single stimuli, the most striking finding is the much lower response probability for very brief stimuli in infants (see Figure 11). Adults require much less stimulation than do infants to achieve equivalent response probabilities. However, at longer durations single stimuli are quite effective in infants, supporting the belief that the sustained system is relatively mature in infants (Graham, Strock, & Zeigler, 1981).

Graham, Strock, and Zeigler (1981) suggest that transient immaturity may be due to both motor system and sensory system immaturity. The response of the orbicularis oculi, the muscle responsible for the eyeblink, to a startle stimulus consists of two components, R1 and R2, which are neurologically dissimilar (Sanes, Foss, & Ison, 1982; Shahanl & Young, 1973). The R1 response is a short latency (5-15 ms) response of motoneurons found in the palpebral segment of orbicularis oculi. This R1 component occurs ipsilaterally to electrical and tactile, but not auditory, stimuli. The R2 component has a longer latency (20-100 ms), and occurs in the orbital segment of orbicularis oculi bilaterally. The neural circuit for R2 is more

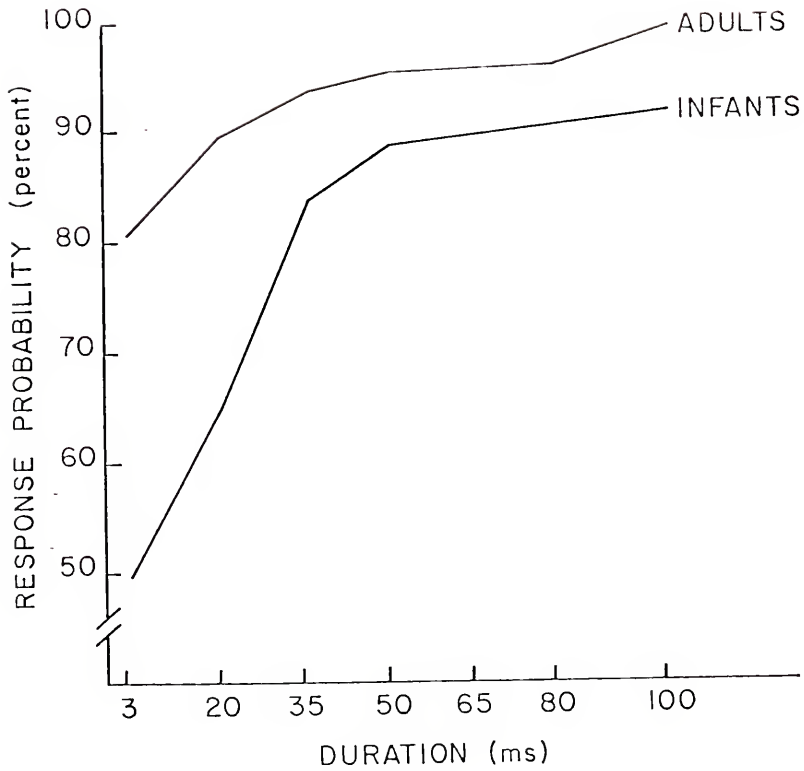


Figure 11. Adult and infant response probability as a function of time for single stimuli.

complicated than that for R1, involving brain stem nuclei at the level of the inferior colliculus. This R2 component is what is measured as the startle eyeblink by a periorbital electrode placement. For this reason, the R1 component may be irrelevant to the present study. This means that the distinction between transient and sustained motoneurons may not be a relevant factor in defining the immaturity of the transient system, contrary to the suggestion of Graham, Strock, & Zeigler (1981). On the other hand, the suggestion by Graham, Strock, & Zeigler (1981) of a neurological dichotomy of transient and sustained sensory neurons is supported by the present research. The fact that pairs of stimuli can be as effective as analogous single stimuli, which contain much more energy, suggests that the input to the startle center may be equivalent for the two types of stimuli. This means that temporal summation occurs either before or at the startle center, due to differential activation of transient and sustained sensory systems.

In a previous report (Blumenthal & Berg, *In press*), it was suggested that startle amplitude and probability may be determined by partially independent underlying mechanisms, a startle trigger and a startle amplifier. This is analogous to the distinction made in cognitive perceptual research between stimulus detection and stimulus identification (Posner, 1978).

The extent to which the two stimuli in a pair of transients have common neural elements may have an effect on their summation. If the units have not fully recovered from the effects of the first pulse, then the contribution of the second pulse may be decreased. This is a type of forward masking, and the recovery of these units may be immature in neonates. This would explain the finding that response

amplitude increases as interstimulus interval increases above 20 ms for infants, but not for adults. This neural recovery may be more extended for the startle amplifier than for the trigger, since no evidence of increase in forward masking was found over the 20-50 ms range of intervals tested, for either infant or adult response probability.

The exact location and nature of the trigger and amplifier mechanisms is unknown, but they are most likely to be found either in the auditory pathway below the inferior colliculus, or in the startle center itself. Also, the two mechanisms may have different locations, since they appear to be partially independent in their responding. If either the trigger or the amplifier is located in the auditory pathway, similar mechanisms may be found in other sensory pathways, and further studies investigating startle trigger and amplifier mechanisms in visual and tactile modalities are suggested. The fact that analogous temporal summation abilities are found across modalities suggests that this summation may be a very useful means of investigating startle trigger and amplifier mechanisms cross-modally. It would also be useful to conduct comparative studies using animals, to more accurately locate the mechanisms underlying these differential findings. Such studies might show that the trigger and amplifier mechanisms are due to specific startle center involvement, or to basic organizing principles found in all sensory systems.

In adults, sensitivity to transients may be greater for the trigger than for the amplifier, since response probability peaks at 20 ms for both single and paired stimuli, while the amplifier continues to summate until 40 ms. This implies that the amount of energy required to reach maximal activation is lower for the trigger than for the

amplifier. In fact, this critical level may be below 20 ms, and further research at durations and intervals of less than 20 ms is needed to measure the transient sensitivity of the startle trigger.

In infants, the immature transient sensitivity of the startle trigger is illustrated by the low response probabilities for brief duration stimuli (see Figure 11). The immaturity of the startle trigger is further illustrated by the fact that pairs of pulses are much less effective in infants than in adults (see Figure 10). However, the infant and adult curves are parallel, so it may be the case that interstimulus interval is not the crucial parameter. The probability data suggest that both the single and paired stimulus functions show age differences which are due to immature responding to very brief stimuli, regardless of the interstimulus interval. Making individual pulses in each pair longer, so that the critical energy could be reached at the shortest interval, is necessary to separate the effects of increasing stimulus duration and interstimulus interval. Future research using pairs of longer stimuli is suggested, to separate these duration and interstimulus interval effects more fully.

The present data support Graham and coworkers (1981) in their belief that the transient system is immature in young infants. The infant response is immature in three ways. First, the window of temporal summation of transients, as illustrated by response amplitude, is wider in infants than in adults. Second, the degree to which brief stimuli elicit the startle response, as illustrated by response probability, is more pronounced in adults than in infants. Third, pairs of brief stimuli are less effective in eliciting transient system activation at all intervals in infants than in adults, allowing

transient and sustained summation to occur together in infants, for response probability.

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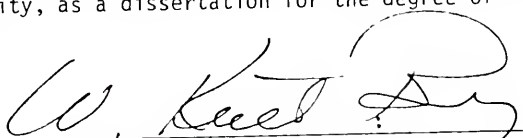
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BIOGRAPHICAL SKETCH

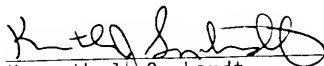
Terry D. Blumenthal was born in Edmonton, Alberta, Canada, on July 17, 1954. He grew up in and around Rolly View, Alberta, and eventually obtained a Bachelor of Science degree, with a specialization in psychology, at the University of Alberta in Edmonton. With this feat behind him, he decided to move from the top of a large pile to the bottom of a smaller pile, and he applied for graduate school. The University of Florida retained his services for five years, during which time he enjoyed life to the fullest, with considerable help from his friends and fellow graduate students in a variety of departments. While at the University of Florida, he worked under the supervision of Dr. W. Keith Berg, who had a profound influence on how Mr. Blumenthal viewed the world. Five years after his arrival in Gainesville, Mr. Blumenthal moved on to a teaching position at Hamilton College in upstate New York, where he taught courses, wrote his doctoral dissertation, and had a very productive year on all fronts. At this writing, matrimony looms on the horizon. Mr. Blumenthal has been consistently reminded of the considerable rewards which follow hard work, personal application, and a well-told joke.

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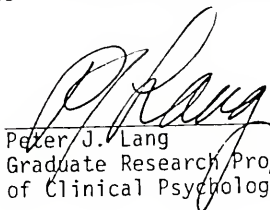
W. Keith Berg, Chair
Associate Professor of Psychology

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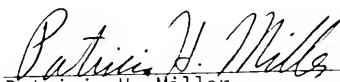
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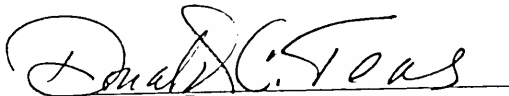
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This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Liberal Arts and Sciences and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1985

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